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The challenges to inferring the regulators of biodiversity in deep time

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Abstract

Attempts to infer the ecological drivers of macroevolution in deep time have long drawn inspiration from work on extant systems, but long-term evolutionary and geological changes complicate the simple extrapolation of such theory. Recent efforts to incorporate a more informed ecology into macroevolution have moved beyond the descriptive, seeking to isolate the generating mechanisms of dynamic signatures and produce testable hypotheses of how groups of organisms usurp each other or co-exist over vast spans of time. This Theme Issue was planned to exemplify this progress, providing a series of case studies of how novel modelling approaches are helping infer the regulators of biodiversity in deep time. In this Introduction, we explore the challenges of these new approaches. First, we discuss how our choices of taxonomic units for study have implications for the conclusions subsequently drawn. Second, we emphasize the need to embrace the interdependence of biotic and abiotic change, because no living organism ignores its environment. Third, in the light of parts 1 and 2, we discuss the set of dynamic signatures that we might expect to observe in the fossil record. Finally, we ask whether these dynamics are the most ecologically informative foci for research efforts aimed at inferring the regulators of biodiversity in deep time. The papers in this Theme Issue contribute in each of these areas.

1. Introduction

Organisms respond to their environments. This link regulates biodiversity, but its complexity confounds efforts to provide unequivocal evidence for supposedly simple expectations. The challenge is to disentangle how environmental, ecological and evolutionary processes interact in deep time when they cannot be observed directly. Palaeobiology and evolutionary biology have long drawn inspiration from methods initially developed for population ecology [1, 2], where the chief regulator of biodiversity is often purported to be density-dependence: population growth rate falls as population size increases due to resource limitation [3]. The co-option of population ecological theory into palaeobiology has a distinguished history [4], but a simple re-interpretation of elementary ecology to the macroecological and macroevolutionary scale is compromised by the vast time scales, which provide scope for environmental, (micro)evolutionary and geological change. Simple plots of species' diversity through time reveal coarse dynamical patterns of how the diversity of life on Earth has fluctuated [5], but do not uncover which underlying mechanisms generate such higher-level patterns [6].

The outcomes of interactions among living organisms can be experimentally manipulated to tease apart direct causes of births and deaths. These interactions can have negative (competition, predation) or positive (mutualism, symbiosis) consequences for a focal species. The outcome of the interactions depends on the abiotic arena in which those species co-exist: the victorious species in ecological competition is the one that can persist on the lowest amount of the limiting resource [7]. It is difficult to move from small-scale experiments to large temporal and spatial scales [8] because of substantial changes in the terms of reference: carrying capacities in population biology restrict population growth directly by resource limitation [3, 9], whereas an analogous limit at supraspecific level, and over hundreds of thousands or millions of years, would be an emergent higher-level phenomenon from genuine interactions among individuals moving together through space and time.

Traditionally, deep-time regulators of biodiversity have polarised into biotic vs. abiotic controls [6], with biotic interactions argued to dominate in the near term and abiotic upheaval imparting the clearer signal over long time scales [10]. The biotic, organismal, ecological perspective is commonly associated with the Red Queen hypothesis originally proposed by Van Valen to explain the apparently age-independent

extinction probabilities among ecologically homogeneous groups [11]. In his original formulation, Van Valen considered the deterioration of the environment to include both the biotic and abiotic environment, but palaeontologists have usually credited most biodiversity change to abiotic factors [10, 12]. The false dichotomy between the supposed superiority of biotic versus abiotic factors in regulating biodiversity [6, 10, 13] echoes the analogous debate in population ecology [9]. While population ecologists concluded that the abiotic environment acts as soft tissue on top of a hard density-dependent "skeleton" [9], ecologists working in deep time have to accept that any purported diversity dependent analogy is an emergent property from accumulating organismal responses to the biotic and abiotic environments with which they interact. These organismal responses are liable to evolve substantially through time.

Evolutionary rates multiply by many orders of magnitude when measured at laboratory scales of days and months, when compared to historical time spans of years and decades and palaeontological spans of millions, or hundreds of millions, of years [14]. Analysts are in effect measuring different aspects of a single fractal phenomenon where some rates are generational changes, while others are the outcomes of phenomena averaged over long-term environmental change. Most palaeontologists will never be as confident as experimental biologists that the individuals and species they study genuinely interacted at a given time in a given location, but that does not mean that it is impossible to study biotic interactions in deep time. Indeed, progress towards more ecologically informed macroevolution has shifted over the past five years from a predominantly descriptive pattern-based approach [15], to one in which we now aim to isolate which ecological mechanisms determined the origination, proliferation and extinction of biodiversity.

This Theme Issue aims to synthesize this progress. Our introduction to the manuscripts, which reviews the state of the art and showcases advances in contemporary modelling and data extraction techniques, lays the foundations required for methods to extract the generating mechanisms. We begin with how our analytical choices affect the results we obtain.

2. Individuals, populations, species and genera

Although ecologists can characterize biodiversity more broadly than simply counting species, most deep-time studies cannot directly quantify abundance or biomass data. A few notable exceptions exist: coarse estimates suggest that biomass [16] and primary productivity [17] might have increased during the Phanerozoic. Additionally, while there are also a few taxon-free approaches used to infer the structure and stability of food webs in deep time [18] and characterize the patterns of ecospace occupancy [19, 20], deep-time investigations into the regulators of biodiversity are, for the most part, limited to counting taxonomic units through time.

Linnaeus wrote in *Fundamenta Botanica* that both genus and species are genuine entities of nature [21]. Mayr [22] argued that species, now considered the canonical unit for macroevolution, obey ecological rules, but conceded that genera also represent a biological reality. The integrated taxonomic evidence that distinct genera occupy morphospace discontinuously and rarely hybridize among themselves due to their long histories of separation [23] support the basic tenet for reproductively isolated taxonomic units. The same could be argued for any higher, clade-based taxa, whatever category names one might wish to apply, provided they reflect fundamentally different organismal constructions.

Acknowledging all the vagaries of matching category terms to clades, Benton [5] showed broadly similar genus and species diversity curves, both of which differed markedly from the corresponding higher order and family curves [See also 24 for an updated version on the Carnivora]. The smoothness at higher taxonomic levels (e.g. families and orders) and the apparent evidence for upper limits to diversity [4, 5] is, in part, a function of artificial constructs (naming by scientists), in part incompleteness and structure of the rock record [25, 26] and also some genuine biotic interactions. A logistic curve at the level of orders or classes might reflect increasing diversification at species level within a continuously branching tree [5], but need not correspond in any simple way to lower-level processes: the marine invertebrates, for example, reach a single equilibrium without the component clades doing so [27].

Given that morphology and species classification within taxa are not necessarily coupled [28], the different diversity trajectories among different levels of the taxonomic hierarchy [5] result in part from taxonomic practices that influence extinction risk [29]. Raup [30] proposed that if species follow Van Valen's law [11] of random extinction with respect to age among homogeneous groups, then genera cannot. There is a

difference between the durations of species and genera because species' longevity is determined solely by extinction, assuming genuine speciation occurred in the first instance, whereas the longevity of a genus is determined by both speciation and extinction of the constituent species. Additional confusion of macroevolutionary longevity arises through pseudospeciation and pseudoextinction [31], which occur when sufficient anagenetic change causes scientists to award a new name to a novel morphological form despite a lack of cladogenetic lineage splitting. These pseudospeciated morphospecies are therefore often named from the anagenetic appearance of a novel character rather than post-speciation divergence from an ancestral species.

To illustrate how taxonomic practices and taxonomic resolution impact our ability to reject fundamental evolutionary laws, we analysed durations of Cenozoic Era macroperforate planktonic foraminifer genera, evolutionary species *sensu* Simpson (defined by the first appearance of a morphological gap, i.e. post-speciation divergence, between sister taxa [29, 31, 32]) and morphospecies (defined by the first appearance of a novel character) compiled by Aze *et al*. [33]. To ensure we were comparing homogeneous groups of species [11], we followed Ezard *et al.* [13] in assigning morphological innovations associated with feeding ecology and depth habitat to each species or genus, and accounted for the changing Cenozoic climate using the Zachos *et al*. [34, 35] $\delta^{18}O$ oxygen isotope compilation of deep sea benthic carbonates and the changing biotic environment using the natural logarithm of the number of contemporaneous morphospecies, evolutionary species or genera (as appropriate). All these explanatory variables were fixed at origination, which encodes the idea that conditions early in a species' or genus' existence leave long-lasting signatures on its duration [36]. Morphospecies and evolutionary species show age-specific patterns of extinction: extinction risk increases with the age of each species [See also 37 for morphospecies. These morphospecies and evolutionary species' results were published in 29.]. The genus durations, on the other hand, cannot be distinguished from Van Valen's law of constant extinction (Fig. 1), although part of that failure to reject is likely due to the much lower sample size of genus vs. species counts. Interpreting these numbers, including the possibility that the age-specific extinction patterns arise due to a veil line (implying we fail to document the shortest-lived species), demonstrates how

analysing different levels of the Linnaean hierarchy can generate different extinction risks during a taxon's existence. Altered extinction risks change species longevities, which, as a consequence, change the strength of any inferred diversity-dependent regulation [29].

The empirical correspondence between the species and genus diversity curves [5] should not therefore be taken to imply that analyses at either species or genus level are equivalent. Genus-level origination encodes substantially more divergent ecologies than those perceived by speciation: higher taxonomy is, in one sense, a crude index of morphological disparity through time [38]. If speciation is in fact a rather easy and common process that constantly produces ecologically similar species [39], then it could be argued that the limits to long-term equilibrium models of diversification [40] are not regulated by speciation but rather by origination of evolutionarily significant units at higher taxonomic levels [41-44]. Equilibrial assumptions are more common for species-level analyses performed by neontologists than analyses on higher taxa [45], which contradicts the empirical paleontological evidence [5] and standard palaeontological practice [4, 27, 46-48].

The assumption that the species is the canonical unit of study has long held, but the inconvenient truth is that a species, like all higher-order taxa in the Linnaean system, contains heterogeneous amounts of intraspecific variation through the spatial organisation of populations and cryptic genetic types. The reality is that genera and species both contain relevant, but distinct, information for what regulates biodiversity over long time scales. The re-emergence of the biological reality of higher taxa has in part been stimulated through the increasing size of molecular phylogenies, and thus statistical power, to identify multiple thresholds which make it clear that molecular diversification cannot be explained by species-level divergences alone [41, 42]. The more resolved level exhibits greater fluctuations [4], which may or may not be of genuine biological interest in terms of identifying the principles behind patterns of biodiversity.

3. Biotic and abiotic contributions to stochastic macroevolutionary dynamics

Sepkoski argued that a stochastic version of his fixed finite upper limit to taxon diversity was "probably more typical of natural systems" than the deterministic analytical solutions [4]. Population ecologists have long used year-to-year fluctuations in abundance to reveal that environmental stochasticity acts on a density-dependent framework [9, 49]. One simplistic partitioning [49, 50] is that the cause of any deviation from a deterministic density-dependent framework is either due to an environmental factor that affects the realised fitness of all individuals concurrently (environmental stochasticity: σ_e^2), or due to winners and losers from particular individual interactions that average out in the long term (demographic stochasticity: σ_d^2). Taken together, year-to-year fluctuations in population abundance can be written as:

$$\sigma_\lambda^2 = \sigma_e^2 + \frac{\sigma_d^2}{N}$$

Demographic stochasticity is defined by a sum of squares statistic for the relative variation among individual fitnesses in a given time interval. Environmental stochasticity is calculated by the residual of observed vs. expected change, minus the difference caused by individual interactions [51], and therefore assumes a uniform response in all individuals (e.g. in our context here, an increase in background origination rates). While this binary classification forms a crass straw man, this simplistic polarisation echoes the palaeobiological dichotomy into either the biotic, organismal Red Queen school [11, 52], or the supposed alternative of an abiotic, environmental Court Jester [12]. The mutual dependence between the hypotheses has only recently been acknowledged [6, 10, 13].

Assuming that the number of species saturates following logistic growth [4], calculating environmental and demographic stochasticity statistics for evolutionary species of Cenozoic Era macroperforate planktonic foraminifera [33] suggests that differential responses among species explains, on average, about three times as much variation as the changing environment (0.087 vs. 0.029). This result is unsurprising. The waxing and waning of relative abundance reported at species [13, 53] and genus levels [27, 54], as well as among higher taxa [55], is evidence that there are always winners and losers from environmental change. In deep time, the key challenge is to identify

why some groups of species are winners and others losers, beyond the patterns that can be generated assuming neutral dynamics [56, 57].

The stochastic population theory used above [49, 51] predicts that environmental stochasticity will dominate dynamics for sufficiently large populations (i.e. *N* large) such that the differences among individuals can therefore be neglected. The species-area relationship is one of the best ecological laws in determining the number of species that can co-exist within a given biome, but, in terms of driving macroevolutionary diversification shifts in deep time, the fragmentation of an area has been argued to be as influential as area per se [58, 59]. In this volume, Jordan et al. [60] find that neutral theory, in which all species are assumed to be functionally equivalent [56] on a fragmenting super-continent cannot explain the post-Jurassic increase in terrestrial species richness. The results suggest a role for some biotic factors, either a competitive advantage or some other founder effect over and above geographic isolation, in the subsequent adaptation and expansion of the clade, even if the precise generating mechanism remains to be identified.

After demographic and environmental stochasticity, the third fundamental cause of stochastic fluctuations in population dynamics is measurement error [50]. Palaeontologists have to worry about the fossils that enter the rocks and which fossils are found [61]. Preservation biases include organismal factors (skeletons or not; slow or fast reproducers; population size), their habitats (marine, river, and lake settings are more often preserved than coasts, uplands and forests), and the subsequent history of the rock (is it eroded or buried; is it metamorphosed or not; is it covered by younger rocks?). Human biases include accessibility (is the rock at the surface; is the rock in reach of people?), geographic location (e.g. Europe vs. South America), and research interest (e.g. diatoms vs. dinosaurs). On the whole, older rocks are less available than younger rocks because the chances of burial under younger rocks increase with age, and much emphasis has been placed on this temporal pattern: Raup [61] and Alroy [27] argue that this bias explains nearly all of the substantial rise in biodiversity through the Phanerozoic, and tie this to a model in which global biodiversity reached modern levels over 400 Myr ago.

The biased distribution of fossils in time and/or space motivated the development of methods to “correct” for the vagaries of the rock record [62-65]. Commonly used sampling proxies, such as counts of collections, localities, or formations, accrue in close

connection with the species count [66]. Residuals-based approaches [64, 65] compare a sampling proxy (e.g. formations count; rock outcrop area) and then identify and remove a sampling trend, with the residuals interpreted as the true biological signal. Acknowledging the limitations of formation counts as a sampling indicator, it remains controversial whether the correlation between rock and species counts, or the residuals from that correlation, represents the holy grail of biological truth [66]. Rarefaction [62] and shareholder quorum subsampling [27] have proven less controversial methods, but still imply that the geological drives the biological. Integrated approaches, which calculate the error due to incomplete preservation and biological diversity simultaneously, promise to place both on an even footing [24, 67-70].

In this volume, Starrfelt & Liow [71] propose a method to identify true levels of bias, and so true levels of former biodiversity, for particular clades in the fossil record. Their new TRiPS method (True Richness estimated using a Poisson Sampling model) is based on the assumption that a particular fossil species, if observed multiple times in a given time interval, has a relatively high probability of fossilization and discovery by palaeontologists. Starrfelt & Liow apply their method to the fossil record of dinosaurs, and estimate that there were 1536 genera and 1936 species of dinosaurs in all, and that the numbers tramping across the Earth at any time ranged up to 300 in the latest Cretaceous, when diversity was highest. The method could revolutionise the ways in which palaeontologists and evolutionists in general treat fossil record data on ancient biodiversity.

The difficulty of extracting the biological signal from the geological noise was formalised by Raup *et al*.'s [72] pioneering work simulating phylogenetic diversification. At a given point in time, Raup *et al*. [72] assumed that each species has an equal probability of going extinct and an equal probability of giving rise to a descendant daughter species. These assumptions evoke the equal-rates Markov model of diversification [57] and Hubbell's Neutral Theory [56] for a clade fluctuating around its supposed equilibrium (assuming, in the latter case, that the birth and death rates are similar). A simple null model with constant rates was able to recover the diversity trajectories seen in the fossil record [72]. "Familiarity with the 'patterns' that random processes create is ... essential" for all scientists [57] because "it is fatally easy to read a pattern into stochastically generated data" [73]. Systematic geological structure can generate seductive impressions on macroevolutionary signals, such as bursts of genus

origination [26], the clumping of last occurrence dates into apparently accelerated extinction events [74] as the ranges of higher-taxa are bounded by mass extinctions [75].

Despite this warning for any literal reading of the fossil record [72], running the same simulations using empirically defined parameter estimates suggested that the fluctuations in fossil taxon counts most likely result from changes in the diversification dynamics rather than a constant-rate stochastic process [76]. Asserting a role for ecological regulators of biodiversity requires the rejection of appropriate null models that incorporate the temporal inconsistencies of fossilisation [57].

4. The regulators and their signatures

Macroevolutionary diversification is the net outcome of speciation and extinction. The regulators of biodiversity act differentially through these two rates as different ecologies compete with each another, filtering global biotic and abiotic environmental change, to shape variation among contemporaneous species in their speciation probability and extinction risk (Fig. 2). Understanding the interplay between organismal biology and environmental change holds the key to identifying the generating mechanisms of macroevolutionary dynamics [13].

Although fossil data are increasingly being used in phylogenetic comparative methods [69, 70, 77], the key interaction between biology and the environment is still rarely incorporated. This is in part explained by the lack of methods, but also by the nature of the data. Phylogenetic studies using only extant taxa often reconstruct evolutionary history from a single time slice and are therefore blind to dynamic associations between biological and environmental change, as well as sequential evolutionary changes that influence the evolutionary fate of lineages [78]. This coupling of the biotic response to abiotic environmental change emphasises one limitation of a simple extrapolation of population ecology theory into a macroevolutionary context. Sepkoski [4] assumed a single fixed equilibrium level of species diversity through hundreds of millions of years, which is a strong assumption if we hypothesise that environmental resources affect the outcome of competition [79] in deep time [46, 80].

Competitive interactions might be the most commonly discussed biotic driver of diversification rate changes. Both origination and extinction rates have been reported as

diversity-dependent and both can generate equilibrial dynamics in biodiversity [4, 81, 82]. At a finer taxonomic resolution than assumed by Alroy [81] or Foote [82], speciation rate seems to respond more closely than extinction rate to changes in within-clade diversity [Fig. 3, see also 13, 46], but this balance of influence need not be constant for all time [82]. Species interactions are increasingly being recognised as capable of leaving an impact on clade diversification through a variety of modes [83, 84] and not simply slowdowns in diversification rate with increasing levels of standing diversity [85, 86].

The dominant mode of macroevolutionary competition likely depends on how we define its arena. Unlike the case in Figure 3, which analyses the whole Canidae family as a homogeneous unit, Silvestro *et al*. [53] reported little diversity-dependent speciation within each Canidae subfamily as a distinct guild [87] and evoked interspecific competition among subfamilies in a broader species pool, in which all species compete for similar resources. Under such a scenario, clade replacement selectively drives less competitive guilds to extinction [87]. This difference between Figure 3 and Silvestro *et al.* [53] leads to the more refined hypothesis that biotic competition *between* closely interacting groups of species will leave a signature in extinction rates, whereas competition *within* closely interacting groups of species will leave a signature in speciation probability.

Developing this line of thought, Marshall & Quental [88] explore the hotly debated question of limits on diversification [40, 80]. Verbal interpretations of a diversity dependence mechanism built into a dynamic carrying capacity exist [40, 89], but an environmental regulator of such dynamic limits has not been identified statistically. Marshall & Quental [88] argue that an appropriate definition of the species pool and the consideration of time-variable carrying capacities could reconcile evidence of bounded versus unbounded diversification. The authors propose a diversity-dependent modelling framework with a carrying capacity varying through time as a result of changing either intrinsic diversification rates or the strength of the diversity-dependent effect. Importantly, their approach allows resolution of a long-standing debate about whether total global biodiversity has been held at equilibrium levels for long spans of time, or whether global biodiversity never reaches such levels.

Biogeographical variation fundamentally restricts such global-level analyses. The latitudinal diversity gradient is one of the most frequently described macroecological

patterns [90], but has not been constant through time [91]. The tropics are cited as acting as both a cradle of and a museum for diversity [92, 93], with the consequence being that these biomes act as net exporters of biodiversity to other regions [93, 94]. In this volume, Fenton *et al*. [95] investigate when and how the modern latitudinal diversity gradient in calcareous zooplankton became established. The authors construct latitudinal diversity gradients in deep time as an independent dataset to assess whether any putative driver has a dominant underlying cause or reflects multiple factors acting in concert [92, 93], including the statistical artefact of the mid-domain effect [96]. Fenton et al. [95] demonstrate no latitudinal diversity gradient at the beginning of the Eocene epoch, but that the modern day pattern was established by the Eocene-Oligocene Transition 33.7 Mya.

If specialist species depend intimately on their native biome to persist, then any climate change that alters the spatial extent of these biomes will rapidly lead to their extinction. Exploring the interactions of species and their geographic ranges over ecological and evolutionary time scales has been hard. In this volume, Villalobos *et al*. [97] explore how species co-occur with other species, and find that in the long term species respond individualistically to major climatic shifts, while more stable climates allowed less phylogenetically variable, yet richer palaeocommunities to settle. The authors calculate phylogenetic fields, the co-occurrence patterns among species and their phylogenetic structure within individual species ranges, for living and extinct mammal species over long spans of time, to explore how individual species interact with predators, prey, and competitors, and with major changes in physical environments.

Although these methods can be readily applied in deep time, reconstructing species interactions is only useful when the spatial distribution of communities can be accurately estimated. The preservational biases of the fossil record are exacerbated when variations through space and time require analytical attention. In this volume, Silvestro *et al.* [98] develop flexible new dispersal-extinction approaches that use fossil data to infer macroevolutionary and biogeographical processes while taking into account the incompleteness (temporal and spatial) of the fossil record [99, 100]. The impact of migration is not symmetric [98, 101], implying a role for biotic interactions among already existing species and the new invaders in determining macroevolutionary fates. A major problem with most methods that use extant data only is the fact that ancestral geographic ranges inferred from phylogenies might be blind to local past

extinction and temporal changes in the asymmetry of dispersal rates. Silvestro *et al.* [98] applied their method to a genus-level empirical dataset of Cenozoic terrestrial plants. Their empirical results suggest a predominant dispersal from Eurasia to North America in the Eocene climatic cooling period, but a higher dispersal from North America to Eurasia during the more stable climatic period between 32 and 14 Ma. The most recent 10 My are characterized by a more symmetric dispersal between both continents, although higher extinction rates in Eurasia.

Empirical studies focus increasingly on geographical range as a predictor of extinction, but evidence is mixed: large geographic range buffers fossil taxa against background extinction [102] and contemporary extinction risk [103], but might be futile in the face of mass extinction [104]. Geographic range forms a composite trait not expressed by individuals but by the populations they form, i.e. is, like a putative upper limit to species richness, another emergent phenomenon from lower-level processes. While space can reveal the extent of a given ecological interaction, and different spatial extents impact the probability of speciation [105] and extinction [49], unpicking any ecological catalyst of macroevolution requires identification of the characters that define a species' functional role in their communities [20].

5. Beyond counts and towards ecological significance.

While most deep-time studies on biodiversity dynamics focus on counting taxa (however defined), such counts have limited ability to indicate ecosystem functioning [106]. Phenotypic traits provide this ecosystem functioning and determine the ecological redundancy of given species within a community [107]. Experimental studies indicate that initial species losses have relatively little impact on the healthy functioning of the ecosystem, but that increasing drops in species richness provoke increasing declines of functioning through non-linear feedbacks [108]. The limitations of taxon counts as a coarse presence/absence metric for inferring the link between organism and its environment have long been acknowledged, as have those of simply measuring abundance. "It is time we stopped simply counting taxa and tracking their numbers over time, and began looking at them, measuring them and estimating their ecological roles" [109]. More informative dimensions exist and better describe the state of a given assemblage or community [95, 106, 110].

Missa & Morlon [111] use computer simulations to show, under Neutral Theory [56] with alternative modes of speciation, that species-area relationships and species-abundance distributions reach their equilibriums after species richness. Phylogenetic patterns of biodiversity either do not (e.g. phylogenetic diversity) or take far longer (e.g. tree imbalance and gamma statistics) to converge. The authors also show that the mode and magnitude of speciation strongly affect the time taken for ecological patterns to reach their equilibrium. The authors conclude: "Given that real metacommunities may not have reached equilibrium in terms of species richness, it would be unwise for users of the Neutral Theory of Biodiversity to continue assuming that other biodiversity patterns, which take even longer to converge to equilibrium, are themselves at equilibrium."

One of the reasons for the resurgence of interest in higher taxa is that they, if robustly defined, are more intimately linked to environmental change than species. The environment moderates both the number of ways that organisms can persist, and also the efficiency of the chosen method: the number of hypercarnivores has been roughly constant through time, despite ongoing turnover in named species [112]. The principal way in which functional types are defined in deep time is by assigning roles to particular characters [113]. Mass extinction events generate high levels of species extinction, but can either slightly reduce [114] or considerably change [115] ecological functioning in the clade. Although taxon diversity and morphological disparity are not always coupled [116], morphological disparity typically saturates more rapidly than taxon diversity counts [117]. Obtaining accurate estimates of intraspecific variation is fundamental to adoption of trait-based approaches for their use in inferring niche breadth and stability, as well as the strength of ecological interactions [118, 119]. Understanding changes in the ecological role of a given species, and studying how trait distributions change more broadly, therefore could reveal species interactions. In this volume, Hsiang et al. [120] describe algorithmic procedures to rapidly extract size and shape phenotypic data in microfossil communities, providing the robust sample sizes from which trait (co)variation can be accurately estimated. Hsiang et al. [120] use their workflow to compare and contrast dendrograms obtained through morphological, ecological, and phylogenetic data. Another potential use is to compare the multivariate morphological data that underpins the dendrograms and so assess the relative contributions of evolutionary or ecological processes via simultaneous alterations to phylogeny,

environment and species abundance. A focus on morphological traits promises to "bind the past and present together" [121] as a common analytical currency for analysis in deep time and the present day. The challenge ahead is therefore to identify ecologically meaningful traits that are incompletely rendered by higher taxon definitions [121, 122].

Although the fossil record is the most direct way to access the role of different regulators [78], it has also, until recently, been blind to preservation of certain body parts and physiological functions that might be ecologically very relevant. Here, Trueman *et al*. [123] review ecogeochemical methods to recover individual scale information from macrofossil remains, and thus study food web structure, nutrient fluxes and population connectivity in contemporary deep sea fish systems. Deep-sea fishes share with fossils many of the problems in extracting trait data: difficult-to-access material and vanishingly rare evidence of direct interactions among individuals. The authors provide a balanced perspective of the potential impact of the approach. While evidence exists that symbiosis influences macroevolutionary dynamics in deep time [13], other areas are less well understood: trace element analysis can indicate population connectivity in the focal modern deep sea fishes, but remain unproven in deep time [123]. Adoption of such techniques to yield data on behaviour and physiology promises a more holistic (beyond morphology) view of the interplay between organism and its environment in deep time.

Selection pressure and long-term rates of evolution are regulated by ecological opportunity [124], but any response to selection depends on individual form [125, 126]. Individual form matters because individuals in species are characterised by a distinctive set of traits, many of which covary. It is not individual traits that survive, reproduce and die, but whole individuals. Selection on one trait can generate a response to selection in others [126], implying that we need multivariate approaches within functional modules [127]. The decoupling of size and wing shape, for example, differs among distinct subfamilies of fossil birds and occurred as a precursor to flight [128]. Despite Simpson's evocative "choppy sea" metaphor of a dynamic adaptive landscape [129], there are "dismally few" empirical estimates of how the constraints imposed by trait covariance evolves during a species' existence [130].

Multivariate changes in ecologically relevant traits offer strong potential to better understand the processes that bridge micro- and macroevolution [131]. If there are no strictly macroevolutionary processes [132], then we need a finer resolution to unpick

the circumstances that promote ecological divergence to become fixed through some speciation events, but not in others. Coarse macroecological proxies, even when calculated as integrated variables over the whole duration of each lineage [133], show negligible explanatory power to predict molecular divergence, albeit among a very limited number of species [134] evoking the hypothesis that molecular divergence is accelerated during speciation events [135]. It is now widely accepted that evolutionary divergence can be rapid [14, 136], and its rate covaries negatively with the interval being studied [14]. While diversity dynamics need the fossil record to understand the dual roles of speciation and extinction [78], fine temporal resolution might reveal that the ecological regulators of biodiversity actually operate chiefly in a punctuated fashion during post-speciation divergence, rather than throughout a species' existence once its ecological role is, to a large extent, established.

6. Conclusion

"It is my hope that future work will not reject the question of competition in macroevolution out of hand, but will explore it with new models that are more sophisticated than coupled logistic equations and can use these accumulating paleontological data to produce far more predictive, and therefore testable, statements about how species replace one another over the vast spans of evolutionary time". [137]

The challenge is not to find a dynamic signature of ecological interactions in macroevolutionary dynamics, but rather to isolate a particular generating mechanism from the many sources of bias, the role of random chance and the disparity of potential outcomes. Continued dialogue and ever-closer union of fossil and modern approaches will prove essential in maintaining this momentum [138]. Price & Schmitz [138] extend the argument that morphological traits "bind the past and present together" [121] to an explicitly functional context, arguing that this focus alongside greater integration across biodiversity research silos will enable scientists to better understand how lower-level ecological and evolutionary processes scale up, and vice versa. It is difficult to separate the role of the biotic and abiotic environments, but recent methodological and data advances showcased within this Theme Issue offer increased hope for a brighter future in which we gain a better understanding of how ecological mechanisms regulate the

interplay between organismal biology and environmental change to drive macroevolutionary dynamics.

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Short Biographies

Thomas H.G. Ezard is NERC Advanced Research Fellow across Ocean & Earth Sciences and the Centre for Biological Sciences at the University of Southampton. He leads a group that investigates the interaction of environmental change and population structure, attempting to contextualise evolutionary and ecological dynamics through a demographic lens. His interdisciplinary group most often develops the interface of mathematical and statistical methods for application in the life sciences. Current projects include an individual-based perspective on macroevolution using fossilised foraminifera, and the drivers of transient booms and busts in human population growth.

Tiago B. Quental is Assistant Professor at the Department of Ecology of University of São Paulo. He leads a research group focused on understanding spatial and temporal patterns of biodiversity and the mechanisms involved in generating species diversity. His research interests are not limited to a specific taxonomic group but are instead motivated by a range of questions and structured around them. At the moment he is particularly interested on understanding the role of biotic interactions on biodiversity changes in deep time. The main tools used to approach those questions are molecular phylogenies, fossil record, ecological data and numerical simulation.

Michael J. Benton is Professor of Vertebrate Palaeontology at the University of Bristol. He researches fossil reptiles of the Triassic, including the origin of the dinosaurs, and is particularly interested in the deep-time evolution of life, especially the roles of mass extinctions and adaptive radiations. He is currently investigating questions concerning the quality of the fossil record, the meaning of long-term global diversity curves in terms of models for the evolution of life, the nature of the Permo-Triassic mass extinction and its role in extinction and in opening opportunities for a massive recovery of life in the Triassic.

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Figure Legends

Fig. 1. Rejection of Van Valen's law in Cenozoic Era macroperforate planktonic foraminifera [33] depends on the level of biological organisation used in analysis. We define the homogeneous group for analysis by controlling for morphotype (presence/absence of keels, symbionts and spines), depth habitat, changes in overall climate [34, 35] and overall standing diversity. The scale parameter determines the curvature in extinction risk according to the Weibull distribution; a value of 1 reduces the Weibull to its simpler exponential distribution of constant extinction risk. Maximum likelihood estimates and 95% parametric confidence intervals are shown.

Fig. 2. Simplified schematic of the main regulators of biodiversity during a snapshot in deep time for a given clade. The strength and existence of interactions can change through time. We do not indicate the impacts of space in the schematic because it is assumed that if species are interacting, then, to some extent, their ranges must overlap. Coloured boxes denote distinct ecological types, which compete amongst each other and respond differentially to the same biotic and abiotic signals.

Fig. 3. Diversity-dependent controls acts more strongly through speciation than extinction in Cenozoic Era planktonic foraminifera [33] and Canidae over the last 40 Myr [53]. Number of species was calculated at the start of each bin and regressed against speciation or extinction rate in the next 1 Myr. Regression lines correct for overdispersion and non-constant variance with the mean. Solid lines indicate statistically significant relationships ($p < 0.01$) while dashed lines indicate non-significant ($p > 0.05$) relationships. See also Table S1 for parameter values.

Figures

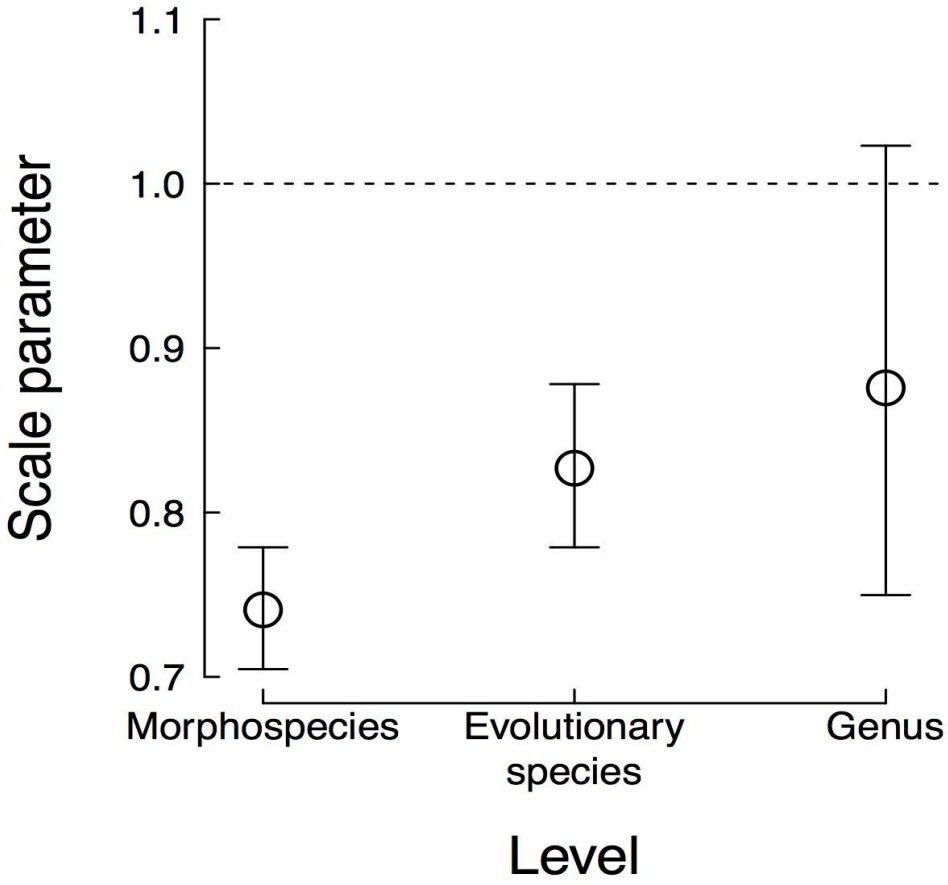

Figure 1.

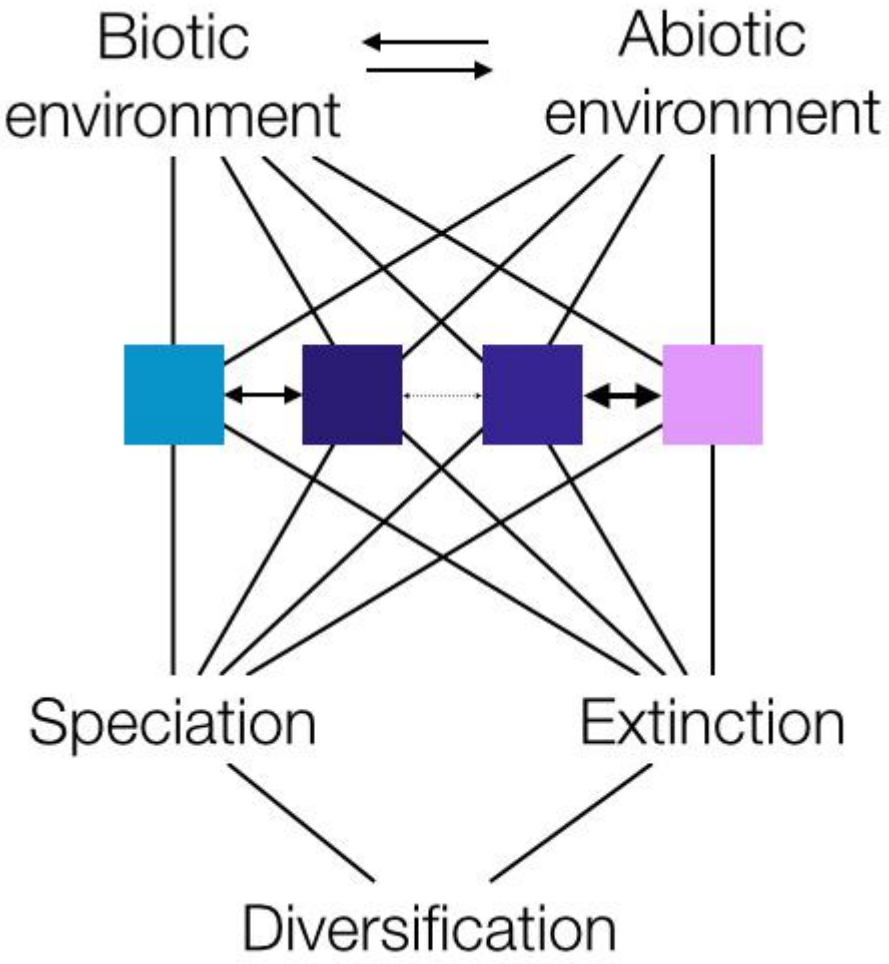
Biotic
environment
Abiotic
environment
Speciation
Extinction
Diversification

Figure 2.

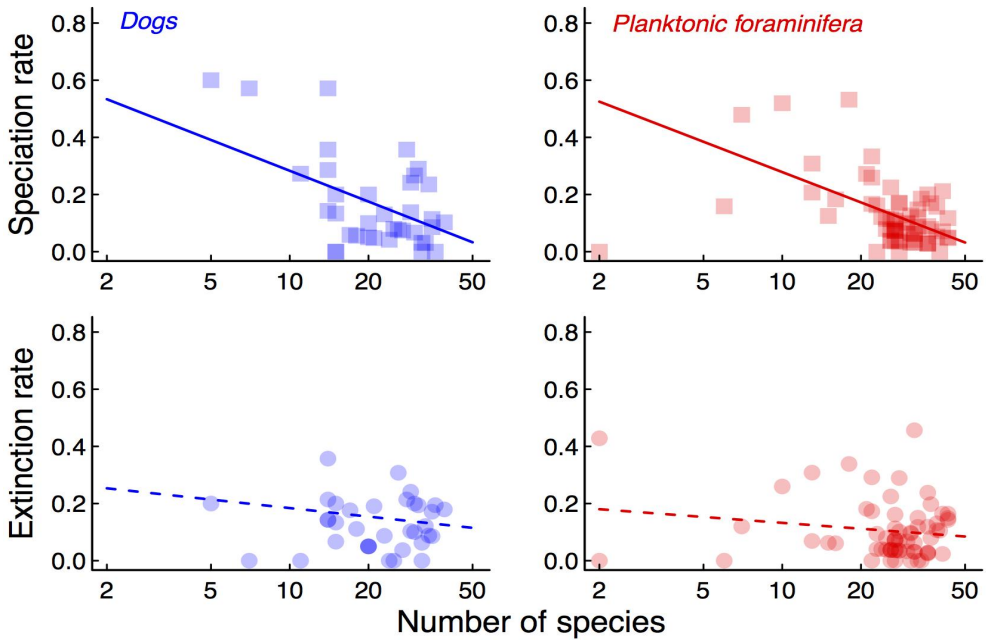
Dogs
Planktonic foraminifera
Speciation rate
Extinction rate
Number of species
0.0
0.2
0.4
0.6
0.8
2
5
10
20
50

Figure 3.

	Morphospecies				Evolutionary Species				Genera			
	coef.	SE	z	p	coef.	SE	z	p	coef.	SE	z	p
Intercept	2.17	0.07	29.39	***	2.33	0.1	22.66	***	3.677	0.349	10.539	***
ln(scale)	-0.3	0.05	-6.48	***	-0.19	0.06	-3.08	**	-0.133	0.155	0.853	
ln(density)	-0.32	0.15	-2.19	*	-0.74	0.26	-2.88	***				
climate	0.11	0.05	2.15	*	0.15	0.08	1.9		-0.132	0.287	-0.458	
spines	0.39	0.09	4.12	***	0.41	0.14	2.86	***	-1.316	0.502	-2.623	***
symbionts												
keels	-0.33	0.14	-2.42	*	-0.39	0.24	-1.63					
ln(density):climate	-0.83	0.14	-5.82	***	0.84	0.32	2.58	**				
keels: climate					0.63	0.23	2.73					
spines:climate									0.873	0.44	1.983	*

Table S1. Coefficients (coef.) with standard errors (SE), z-values and p-value codes for explanatory variables correlated with extinction risks of morphospecies (N=339), evolutionary species (N=210) and genera in planktonic foraminifera (N=48). P-value codes are p > 0.05; * p < 0.05; ** p < 0.01; *** p < 0.001. Where no values are given, this variable was not significant for that model; where no p-value code is given, that term was not statistically significant on its own. These tables for morphospecies and evolutionary species were first published in [29]; the genus level analyses are new. The maximum likelihood estimate of the ln(scale) coefficient for the full model, i.e. without model simplification, is -0.304 with a standard error of 0.158 for a 95% confidence interval on the original scale of (0.537, 1.014). According to the parameterization of the Weibull distribution used, the instantaneous risk (hazard) h of extinction at age x is